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Loss and recovery of carbon and nitrogen after mangrove clearing

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A B S T R A C T

Offsetting carbon (C) emissions and reducing nitrogen (N) pollution have been goals of mangrove restoration programs around the world. There is a common, yet dubious expectation that mangrove restoration will result in immediate and perpetual delivery of ecosystem services. There are expected time lags between mangrove clearing and C and N losses, and between restoration and C and N gains. Obtaining accurate rates of losses and gains requires frequent and long-term sampling, which is expensive and time consuming. To address this knowledge gap, we used a chronosequence of mangrove forests in mangroves in Matang Mangrove Forest Reserve (MMFR) in Malaysia, a region with one of the most C dense forests in the world. In this site, we assessed the ecosystem C and N stocks, including soil, downed wood, downed litter, and trees. The objective was to measure C and N changes through time. After mangrove clearing, C and N losses in soil and downed wood were rapid, with stocks halved after just one year. In the first 10 years after replantation, the forest recovered quickly, with rates of C accumulation of 9.5 Mg C ha^{-1} yr^{-1}. After ten years, the rate of accumulation decreased to 2.8 Mg C ha^{-1} yr^{-1}. However, 40 years after replantation, mangroves were still about 26% lower in C and 15% lower in N compared to our reference forest. The trajectory of recovery of C and N stocks in these forests was different among mangrove components: forest litter recovered rapidly, but downed wood and soil recovered much slower. Programs aimed at reducing C emissions and N pollution should consider that there are temporal lags and ecosystem trade-offs when assessing the effectiveness of mangrove protection and restoration as climate change mitigation strategies.

1. Introduction

Mangrove forests are considered key ecosystems in mitigation programs aimed at reductions in carbon (C) emissions (Murdiyarso et al., 2015) and nitrogen (N) pollution (Mitsch and Gosselink, 2015). Mangrove forests sequester more C and N per area than most terrestrial ecosystems (Donato et al., 2011; Adame et al., 2015a). Contrary to terrestrial forests, mangroves store the majority of their C and N not as plant biomass, but in the soil, where stocks can remain stable for centuries (Adame and Fry, 2016). Mangrove deforestation results in changes in C and N fluxes to the coast (Lee, 2016) and the release of large amounts of C (Alongi et al., 1998; Lovelock et al., 2011). Mangrove restoration has the potential to offset these C and N losses (Alongi, 2012; Ouyang and Guo, 2016).

Throughout the world, numerous mangrove restoration programs are underway, including Mexico (Zaldívar-Jiménez et al., 2010), U.S.A. (Lewis, 2001), East Africa (Kairo et al., 2001), Sri Lanka (Kodikara et al., 2017), and the Philippines (Walton et al., 2007). The expectation of these programs is to restore ecosystem services (Lee et al., 2014; Adame et al., 2015b). Restoration goals include increased coastal protection (Kodikara et al., 2017), pollution reduction (Ouyang and Guo, 2016), and C emission mitigation (Alongi, 2012). The success of restoration programs is usually assessed, if at all, as the establishment of mangrove seedlings after planting (Ellison, 2000; Kodikara et al., 2017). However, even when established, juvenile mangroves might not immediately provide the expected ecosystem services (Koch et al., 2009). In order to assess the success of restoration programs, it is important to consider time lags between perturbation, restoration, the return of ecosystem services.

Loss of C and N is likely to occur within the first years after perturbation, while sequestration occurs within the scale of decades (Marchand, 2017). To assess loss and recovery rates of C and N, frequent and long-term sampling is required, which is expensive and time consuming. The lack of adequate data obtained within realistic time

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frames constrains the capacity of mangroves to participate in C and N markets (Alongi, 2011) and creates false expectations that ecosystem services can be immediately and perpetually restored (Koch et al., 2009).

In this study, we sampled a chronosequence of mangroves in the managed forest of Matang Mangrove Forest Reserve (MMFR), Malaysia. The MMFR is the only mangrove forest in the world with a century-long history of managed forestry (Shaharuddin et al., 2005). The MMFR is managed for timber harvesting and comprises mangrove plots of various ages, from recently cleared plots to those that were never clear-cut and are almost a century old. We took advantage of this setting to study how C and N in forest litter, downed wood and soil respond to perturbation, in this case, clear-cut harvesting. We also collected published information on soil and tree C from previous studies in MMFR. The aim was to quantify the loss of C and N after mangrove clearing, the temporal trajectory of recovery, and the potential pathways of gains and losses. This information will provide a realistic time frame for the assessment of restoration success and the fair valuation of mangrove forests in one of the most C dense regions in the world (Atwood et al., 2017).

2. Materials and methods

2.1. Study site

The MMFR is located near the town of Kuala Sepatang (4°50'17.7″ N; 100°37'51.7″ E) on the northwest coast of Perak State, Peninsular Malaysia (Fig. 1). The MMFR lies on deltaic sediments fed by the three major local rivers: Sepetang, Larut and Terong Rivers. The MMFR has 40,288 ha of mangrove forests, from which 75% are managed for the production of charcoal and poles. The MMFR includes 569 ha of forest that has never been clear-cut, although had some isolated tree harvesting 70 years ago. This forests, hereafter "reference" forest, supports a high tree diversity. The MMFR also has an old-growth forest of 40 + years set aside for education purposes.

Forests in MMFR are currently managed on a 30-year rotation cycle with 110 defined compartments or management units (Shaharuddin et al., 2005). Approximately 1000 ha of mangroves are harvested annually. One to two years after tree harvest, the forest is replanted with seedlings of *Rhizophora apiculata*. At 15 years, the forest is thinned, cutting small trees around a radius of 1.2 m and at 20 years, the forest is thinned a second time by cutting trees around a radius of 1.8 m (Shaharuddin et al., 2005). The managed forests are homogeneous and mostly monospecific stands of *R. apiculata*, with a few trees of *R. mucronata, Bruguiera parviflora, B. gymnorhiza* and *B. cyclindrica*. The virgin forest is a mixture of the above species plus 22 other mangrove species (Shaharuddin et al., 2005). Mangrove soils at 0–30 cm depth are mainly composed of clay (50–56%) and silt (20–30%) with a low pH (3.2–4.2), and high organic content (40–70%; Azani et al., 2005).

The region containing the MMFR has a wet humid climate, primarily influenced by two monsoons, the southwest monsoon, which usually arrives in May and lasts until September, and the northeast monsoon, which lasts from November to March. The mean rainfall of the region is between 200 and 400 mm per month, with the months of October and November being the wettest (Malaysian Meteorological Department, 2017). Annual mean water temperature of the Sepetang River is relatively constant at 29 °C; pH values of the water range from 6.8 to 7.2, and salinity ranges from 15.1 ± 0.1 upstream to 24.5 ± 0.5 in coastal waters (Ramarn et al., 2012). Tides are semi-diurnal, mesotidal, with mean high levels of 2.69 m and 2.06 m for spring and neap tides, respectively (NHCM, 2017).

2.2. Site selection and sampling

Field sampling was conducted in February 2016. A range of mangrove sites of different ages was sampled to assess changes in C and N stocks through time. The selected sites were close to each other (< 5 km apart) and had similar salinity and nutrient inputs (Katsuhisa and Choo, 2000). The six sites ranged in age as follows: (1) one year after harvesting, hereafter "clear-cut "site (Block P-14-24 in compartment 19), (2) five years after replantation (Block P-10-119, compartment 31), (3) 15 years after replantation (Block P-00-107, compartment 44), (4) 30 years after replantation (Block P-15-165, Compartment 19), (5) an old-growth forest of 40 years reserved for educational purposes (43 ha), and finally, (6) a 70 year-old reference forest (Fig. 1, Table 1). All forests fringed a main river channel, except the 40 year-old forest, which fringed a smaller creek (Reba River).

At each site, a 100 m-transect perpendicular to the water edge was established following the methodology of Kauffman and Donato (2012). This sampling design considers that the variation in mangrove structure and biomass is mainly driven by tidal inundation (Lugo and Snedaker, 1974). Within each transect, we established six plots of 7 m in radius at 25 m intervals. In the clear-cut site, the intervals were 10 m because the cleared patch was < 100 m in width. At each plot, we collected samples to measure C and N in forest litter, downed wood, and soil as explained below.

2.2.1. Forest litter

Forest litter was collected at each plot in duplicates with 40 × 40 cm quadrats established at opposite sides of the transect. The litter from each quadrat was rinsed, air-dried for 48 h, and weighed. A representative subsample of ~10 g was taken to the laboratory, where it was dried at 60 °C and reweighed. The amount of biomass was estimated as dry weight per area (ha). Forest litter biomass was converted to C and N stock on the basis of its C and N content, which was measured with an elemental analyser coupled to an isotopic ratio mass spectrometer (EA-IRMS, Sercon System, Griffith University).

2.2.2. Downed wood

Downed wood was sampled at each plot with the planar intersect technique (Brown et al., 1982) adapted for mangroves by Kauffman and Donato (2012). The wood pieces were sorted into three categories: small (< 2 cm width), large-sound, and large-rotten. Wood density was measured from 50 pieces of wood collected across sampling sites as dry weight divided by volume measured as water displacement. The C content in the downed wood was estimated by multiplying the mean wood biomass by a factor of 0.5 (Kauffman et al., 1995) and by a factor of 0.005 for N (Gong and Ong, 1990; Romero et al., 2005). In the 5 and 15-year old plots, recently downed wood was separated from downed wood from the previous harvest, which was clearly identified because widths of older downed wood were larger than those of standing trees.

2.2.3. Soil

In each plot, a soil core of one-meter length was taken with a stainless steel open auger of 6.4 cm diameter (1609 cm^3) attached to a cross handle. Soil samples of known volumes were collected at each plot (n = 5 per site) from at least four depths (0–15, 15–30, 30–50, > 50 cm). To assess small-scale variability with depth, we collected an extra core at each site and divided it to six depths (0–10, 10–20, 20–30, 30–40, 40–50, > 50 cm). Interstitial salinity was measured from the water within the hole from where the core was retrieved. Salinity was measured with a hand-held refractometer (ATAGO Master-S/Millα). Soil depth was estimated by inserting a 2-m aluminium rod of 1 cm in diameter in the soil and measuring the depth of the horizon between organic matter and parental bedrock material. The soil samples were air-dried in the field, and then oven-dried in the laboratory at 60 °C. Bulk density was calculated by dividing dry weight by volume of the sample. Roots were not removed from the soil samples, thus the soil includes live roots recently produced and dead roots preserved in the soil, which usually comprise most of the soil OC in mangrove forests (Adame et al., 2017). To reduce costs of analysing a large number of soil samples (n = 163), two-thirds of the samples

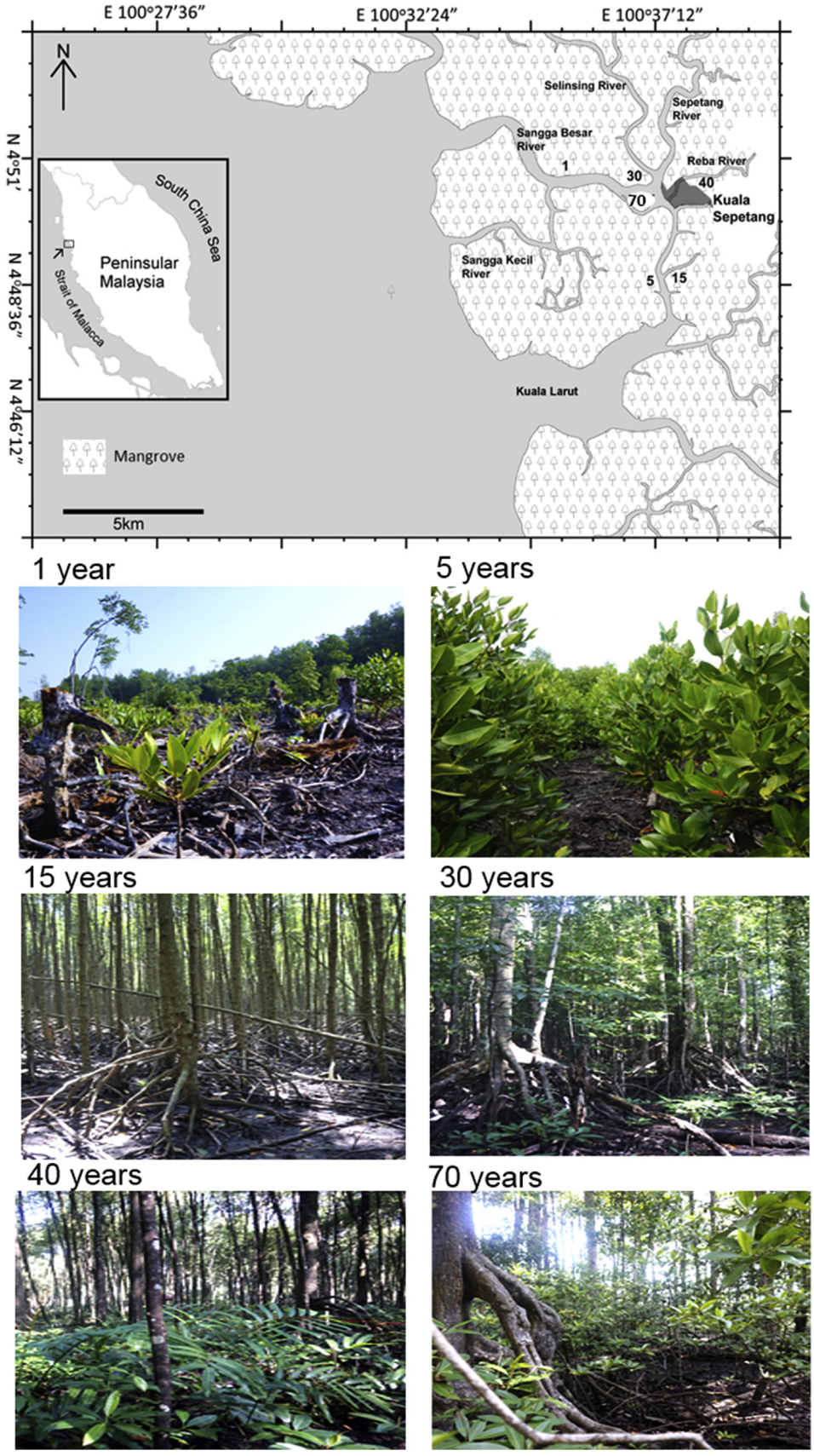

Fig. 1. Sampling locations in the Matang Mangrove Forest Reserve, Peninsular Malaysia. Sampling sites are indicated by numbers corresponding to years after clear cutting; 1 – clear-cut or one year after tree harvest, 5-year old mangroves, 15-year old mangroves, 30-year old mangroves, 40-year old mangroves, and a 70- year old mangrove, which was considered the reference forest.

Table 1
Characteristics of mangrove forests in Matang Mangrove Forest Reserve, Malaysia.

Location	Stand age	Stand description	Interstitial salinity (ppt)
4° 50.714′ 100° 35.937′	0 ("clear-cut")	Harvested	14.8 ± 0.6
4° 48.914′ 100° 37.297′	5	Planted	9.3 ± 0.3
4° 49.157′ 100° 37.531′	15	Planted	9.7 ± 0.2
4° 50.651′ 100° 37.287′	30	Planted and thinned	8.7 ± 0.6
4° 50.527′ 100° 38.196′	40	Reserved	7.7 ± 0.8
4° 50.292′ 100° 37.189′	> 70 ("reference")	Reserved	7.7 ± 0.5

(n = 103; plots 1, 3 and 5 at each site) were analysed for %C and %N (EA-IRMS, Sercon System, Griffith University). Additionally, all the samples were analysed for organic matter (OM) using the loss of ignition method (Heiri et al., 2001). There is a strong correlation between organic carbon (OC), OM and bulk density (e.g. Adame et al., 2016, Fig. 1S) from which we calculated the rest of the OC values. All soil samples were corrected for inorganic C (Heiri et al., 2001), although in all samples it was low (< 10%).

2.2.4. Ecosystem C stocks

To estimate ecosystem C stocks we compiled published data on tree biomass within the MMFR (Table 1S). Mean tree biomass with forest age is quite consistent due the design of the planting and managing of the forest. For example, forest yields between 1980 and 1989 were 177 tonnes ha^{-1}, between 1990 and 1999 were 175 tonnes ha^{-1}, and between 2000 and 2009 were 179 tonnes ha^{-1}. Tree biomass from plots of different ages was obtained from published values of biomass (which were estimated from diameter at breast height and allometric formulas) by Ong et al. (1984), Gong et al. (1984), Putz and Chan (1986), Alongi et al. (2004), Goessens et al. (2014), Hazandy et al. (2014) (Table 1S). Tree C stocks were obtained by multiplying tree biomass by a factor of 0.48 (Kauffman and Donato, 2012). Tree N stock was obtained by multiplying biomass content by 0.005 (Gong and Ong, 1990). Tree C and N stock were added to forest litter, downed wood, and soil to estimate changes in ecosystem stocks through time.

2.2.5. Origin, stability, and decomposition of soil C

We analysed 103 samples for $\delta^{13}C$ and $\delta^{15}N$, which are ratios of light and heavy isotopes, which are useful proxies of C and N origin and soil decomposition (Adame and Fry, 2016). The most likely sources of C and N from mangrove soils are mangrove material (roots, wood and litter) and phytoplankton transported during tidal inundation (Adame and Fry, 2016). We analysed 14 samples of mangrove litter fall from each site. Phytoplankton were sampled along the Sepetang River at 11 locations by filtering water through a 20-μm-mesh plankton net. In the laboratory, phytoplankton was retained by filtration onto pre-combusted Whatman GF/C glass fibre-filters.

Mangrove soils, litter and phytoplankton were analysed with an elemental analyser coupled to an isotopic ratio mass spectrometer (EA-IRMS, Sercon System, Griffith University, and ANCA-SL -Europa 20-20, Marine Biological Laboratory, Woods Hole, U.S.A). The analytical standard deviation of the standards were < 0.1‰ for $\delta^{13}C$ and < 0.2‰ for $\delta^{15}N$. The stability of the soil C and N was determined from the variation of the $\delta^{13}C$ and $\delta^{15}N$ values within depth of mangrove stands of different ages. We expected that if C and N amounts were stable, their isotopic values will remain constant with depth; if the soil was perturbed after tree harvest, $\delta^{13}C$ values should become enriched as a result of increased decomposition (Nadelhoffer and Fry, 1988; Adame and Fry, 2016).

2.3. Statistical analyses

Linear regressions were conducted to assess the relationship between %C and %N (dependent variables) and bulk density and %OC (explanatory variables) using linear regressions (SPSS v24, IBM, New York, USA). To obtain rates of C and N accumulation, we modeled the stock of C and N as an additive function of time using generalised additive models (Wood, 2011). We used a Gaussian distribution and thin-plate regression spines for the two predictor variables. We set the k parameter (upper limit on effective degrees of freedom) to 5 for all components. We chose this value of k because it was sufficient to all non-linearities in the splines and this value also ensured the model assumptions were met (Wood, 2006). Predicted C and N stock values were given as means for the average plot, with standard errors. We also used the generalised additive models to estimate the change in the tree and soil C stocks over time from values obtained from the literature for the MMFR. C and N sequestration rates were estimated from the changes in time of the mean predicted values.

To compare isotope values among forests of different ages and among soil depths, we used depth and age as fixed factors and plot as the random factor of the ANOVA model. Normality was assessed with probability plots and the Shapiro-Wilk test. When the variable was not normally distributed (e.g. $\delta^{15}N$), it was transformed ($\log_{10}$ x). When transformations were not enough to achieve normality (e.g. N:C), the samples were analysed with the non-parametric Kruskal Wallis test. Statistical tests were performed with R and SPSS Statistics (v24, IBM, New York, USA). Values reported are means and standard errors, unless specified otherwise.

3. Results

3.1. Forest litter

Forest litter biomass ranged between 1.7 ± 0.5 Mg ha^{-1} in the 5 year-old forest to 3.7 ± 0.7 Mg ha^{-1} in the 30 year-old forest. The litter accumulated in the floor corresponds to a minimum of 0.78 ± 0.2 Mg C ha^{-1} and 0.02 ± 0.00 Mg N ha^{-1} and a maximum of 1.7 ± 0.3 Mg C ha^{-1} and 0.03 ± 0.01 Mg N ha^{-1} (Table 2). The C accumulation of forest litter was highest during the first eight years

Table 2
Carbon (Mg C ha^{-1}) and nitrogen stock (Mg N ha^{-1}) in forest litter and downed wood from mangrove forest of different ages in the Matang Mangrove Forest Reserve, Malaysia. The clear-cut site had no forest litter one year after tree harvest. In the 5 and 15 year-old forests, natural downed wood was separated from downed wood of previous harvest (width of wood > DBH of standing trees).

	5 years	15 years	30 years	40 years	70 years
Forest litter					
C stock	0.78 ± 0.22	1.48 ± 0.29	0.93 ± 0.15	1.66 ± 0.30	1.31 ± 0.25
N stock	0.02 ± 0.00	0.03 ± 0.01	0.02 ± 0.00	0.03 ± 0.01	0.03 ± 0.01
Downed wood					
C stock	10.4 ± 2.3	15.3 ± 2.8	35.1 ± 5.9	29.6 ± 12.1	62.7 ± 10.7
N stock	0.11 ± 0.02	0.15 ± 0.03	0.35 ± 0.06	0.30 ± 0.12	0.63 ± 0.11

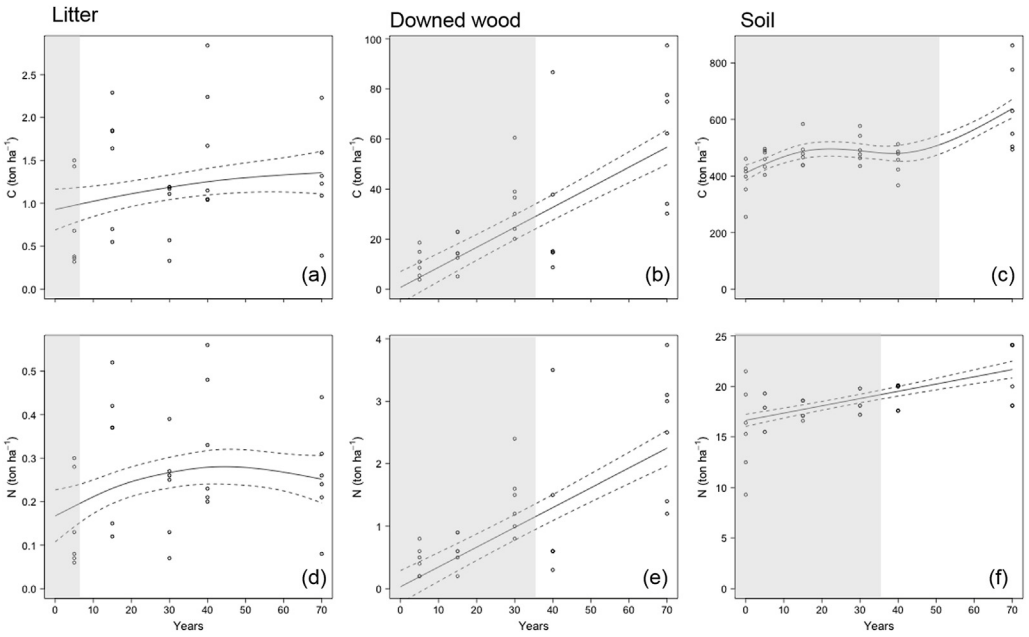

Fig. 2. Carbon (C) and nitrogen (N) stocks (Mg ha^{-1}) after mangrove replantation for (a,d) forest litter, (b,e) downed wood, and (c,f) soil in Matang Mangrove Forest Reserve, Peninsular Malaysia. The dotted lines represent standard errors and the shaded area shows the period after which 50% of the original stock has been recovered.

with 0.01 ± 0.00 Mg C ha^{-1} yr^{-1}, then decreased to values ≤ 0.005 Mg C ha^{-1} yr^{-1} after 42 years (Fig. 2a). Similarly, N accumulated at a rate of 0.004 ± 0.000 Mg N ha^{-1} yr^{-1}in the first 15 years, and at rates ≤0.001 ± 0.000 Mg N ha^{-1} yr^{-1} from 34 years onwards (Fig. 2d). At seven years, the amount of forest litter was 50% of the original stock in the reference forest. The clear- cut site had no forest litter, thus, one year after tree harvest, 0.93 ± 0.15 Mg C ha^{1} and 0.02 ± 0.00 Mg N ha^{-1} of forest litter was lost from the forest, either by decomposition, consumption or tidal exchange.

3.2. Downed wood

The density of small pieces of downed wood averaged 1.09 ± 0.1 g cm^{-3}, the density for large-sound wood averaged 1.24 ± 0.1 g cm^{-3}, and for large-rotten wood averaged 0.71 ± 0.1 g cm^{-3}. Downed wood stocks ranged from 10.4 to 62.7 Mg C ha^{-1} and from 0.11 to 0.63 Mg N ha^{-1} for the 5 year old and reference forest, respectively (Table 2). Downed wood accumulation increased linearly with age with a constant mean rate of 0.80 Mg C ha^{-1} yr^{-1} and 0.07 Mg N ha^{-1} yr^{-1} (Fig. 2b, e). At 35 years, the amount of downed wood was 50% of the original stock (Fig. 2b,e). The clear-cut and the 5 year-old mangrove had 76 and 58 Mg ha^{-1} of downed wood biomass from the previous harvest, respectively, so five years after tree harvest most of the downed wood was still decomposing in the mangrove floor. At 15 years, the downed wood from the previous harvest had mostly disappeared.

3.3. Soil

Mangrove soil was deeper than 2.5 m at all sampled sites. Soil %OC and %N increased with forest age (Table 3). Lowest values were measured in the surface of the clear-cut stand with 6.3 ± 0.5 %OC and 0.35 ± 0.02 %N; highest %OC values were measured in deep soils (50–100 cm) of the reference forest with 19.4 ± 0.9% and highest %N was measured in the surface of the 30-year old forest with 0.79 ± 0.14%. Bulk density ranged between 0.26 ± 0.02 g cm^{-3} in the 30-year old forest and 0.43 ± 0.03 g cm^{-3} in the clear-cut forest (Table 3). In all samples, the inorganic C fraction was < 10% of the total C, but usually < 5%. Soil bulk density was significantly correlated with %OC and %N (y = -43.3x + 29.6, R^2 = 0.62, p < 0.001; and y = −1.15x + 0.94, R^2 = 0.53, p < 0.01, respectively, Fig. S1), so that high %OC and %N was measured in soil with low density. Soil %OC and %N were also correlated with soil %OM, but only when the clear-cut site was excluded (y = 0.37x – 0.063, R^2 = 0.61, p < 0.001; and y = 0.013x + 0.063; R^2 = 0.78; p < 0.001, respectively, Fig. 1S).

The clear-cut mangrove soils had 29.3% less OC and 24.2% less N than the reference mangrove forest, suggesting that after clearing a forest, about a third of soil OC and a fourth of soil N is lost. Additionally, the clear-cut forest had 18.7% less C and 14.4% less N than the forest at 30 years, suggesting that clearing a managed forest causes the loss of about a sixth of the soil C and N. Soil OC and N loss in the clear-cut site was observed throughout the sediment column to depths of up to 1 m (Table 3).

Soil OC and N stocks increased with forest age from 385.2 ± 72.6 MgC ha^{-1} and 15.7 ± 1.80 MgN ha^{-1} in the clear-cut site to 545.0 ± 113.4 MgC ha^{-1} and 20.73 ± 1.77 MgN ha^{-1} in the reference forest (Fig. 2c, f). The highest soil OC stock was measured in the reference forest ($F_{5,25}$ = 5.86, p = 0.001). Soil OC accumulation was 5.7 ± 0.2 MgC ha^{-1} yr^{-1} in the first ten years after replantation, which decreased to ≤5 Mg C ha^{-1} yr^{-1} until 40 years. After 40 years, accumulation rates were variable between 0.2 and 7.6 Mg C ha^{-1} yr^{-1}, probably due to low C stocks in the 40 years forest (Fig. 2c). When analysing our soil C stocks with those estimated from published data (Alongi et al., 2004) we found accumulation rates of 2.9 ± 0.0 Mg C ha^{-1} yr^{-1} in the first ten years decreasing to rates ≤ 1.2 Mg C ha^{-1} yr^{-1} after 50 years (Fig. 3b). Soil N accumulation followed a linear trajectory, with a constant accumulation rate of 0.07 Mg N ha^{-1} yr^{-1} (Fig. 2f). It took about 50 years for soil OC and about 35 years for soil N to recover half of the losses after clearing (Fig. 2c and d, 3b).

3.4. Ecosystem C and N stocks

The trajectory of tree C stocks was analysed from published data (Table 1S). Tree C accumulation was 4.4 ± 0.0 Mg C ha^{-1} yr^{-1} in the first 12 years, decreasing to values ≤ 1 Mg C ha^{-1} yr^{-1} after 62 years. It took 24 years, for the forest to reach half of the reference tree C stock (Fig. 3a).

Total C and N stocks (including forest litter, downed wood, soil and trees) generally increased with forest age from 385.2 ± 72.6 Mg C ha^{-1} and 15.7 ± 1.8 Mg N ha^{-1} in the clear-cut forest, to maximum values of 895.8 ± 113.9 Mg C ha^{-1} and

Table 3
Soil organic carbon (%OC), nitrogen (%N), bulk density (g cm^{-3}), organic carbon and nitrogen stocks (Mg ha^{-1}) up to 1 m and extrapolated to 2.5 m for mangrove stands of different ages in the Matang Mangrove Forest Reserve, Malaysia. BD = bulk density. Values are means ± standard error of six plots.

Depth (cm)	%OC	%N	BD (g cm^{-3})	OC stock (Mg C ha^{-1})	N stock (Mg N ha^{-1})
Clear-cut					
0–15	6.3 ± 0.5	0.35 ± 0.02	0.46 ± 0.03	41.3 ± 5.8	2.41 ± 0.26
15–30	6.9 ± 0.7	0.37 ± 0.02	0.48 ± 0.02	51.2 ± 4.1	2.60 ± 0.13
30–50	11.0 ± 0.9	0.42 ± 0.03	0.41 ± 0.02	88.6 ± 6.4	3.50 ± 0.23
50–100	11.5 ± 0.9	0.44 ± 0.02	0.36 ± 0.02	204.2 ± 20.7	7.19 ± 1.72
Total: 0-100				385.2 ± 72.6	15.70 ± 1.80
Total: 0-250				1018 ± 33.0	33.0 ± 6.05
5 years					
0–15	8.8 ± 1.5	0.39 ± 0.01	0.47 ± 0.03	58.7 ± 9.6	2.58 ± 0.25
15–30	8.8 ± 1.2	0.40 ± 0.01	0.45 ± 0.02	61.3 ± 5.1	2.66 ± 0.32
30–50	11.8 ± 2.1	0.46 ± 0.02	0.42 ± 0.02	96.8 ± 3.5	3.64 ± 0.17
50–100	14.3 ± 1.6	0.47 ± 0.04	0.35 ± 0.01	244.0 ± 6.2	8.66 ± 1.12
Total: 0-100				460.8 ± 14.8	17.50 ± 1.10
Total: 0-250				1234 ± 18.0	40.1 ± 4.06
15 years					
0–15	16.8 ± 1.7	0.64 ± 0.07	0.30 ± 0.03	69.3 ± 7.0	2.63 ± 0.28
15–30	14.4 ± 1.3	0.58 ± 0.08	0.36 ± 0.02	79.3 ± 3.7	2.87 ± 0.38
30–50	17.0 ± 1.0	0.54 ± 0.06	0.33 ± 0.02	111.5 ± 3.6	3.81 ± 0.03
50–100	16.6 ± 1.1	0.54 ± 0.04	0.27 ± 0.01	223.1 ± 14.3	8.14 ± 0.74
Total: 0-100				483.2 ± 22.1	17.45 ± 0.62
Total: 0-250				1169 ± 68.8	40.51 ± 3.19
30 years					
0–15	18.1 ± 1.6	0.79 ± 0.14	0.26 ± 0.02	67.8 ± 4.3	2.80 ± 0.32
15–30	18.2 ± 1.7	0.66 ± 0.04	0.29 ± 0.02	77.4 ± 5.1	2.71 ± 0.18
30–50	17.2 ± 1.7	0.67 ± 0.06	0.31 ± 0.02	104.7 ± 7.6	3.97 ± 0.37
50–100	17.6 ± 1.1	0.61 ± 0.06	0.29 ± 0.02	247.6 ± 8.9	8.86 ± 0.32
Total: 0-100				497.5 ± 21.5	18.35 ± 0.75
Total: 0-250				1240 ± 45.2	44.95 ± 1.72
40 years					
0–15	11.1 ± 1.9	0.47 ± 0.10	0.41 ± 0.06	56.5 ± 5.2	2.95 ± 0.19
15–30	10.5 ± 2.2	0.45 ± 0.11	0.41 ± 0.04	54.9 ± 6.3	2.42 ± 0.12
30–50	10.3 ± 1.9	0.44 ± 0.09	0.47 ± 0.03	79.5 ± 12.3	4.21 ± 0.61
50–100	13.5 ± 2.2	0.53 ± 0.07	0.42 ± 0.02	252.3 ± 25.3	9.69 ± 0.78
Total: 0-100				454.3 ± 21.3	19.26 ± 0.83
Total: 0-250				1187 ± 100	48.5 ± 4.23
Reference (70 years)					
0–15	18.5 ± 1.0	0.72 ± 0.02	0.31 ± 0.01	70.1 ± 14.4	3.45 ± 0.16
15–30	18.3 ± 1.1	0.73 ± 0.03	0.32 ± 0.03	79.8 ± 16.7	3.75 ± 0.36
30–50	17.7 ± 1.0	0.68 ± 0.03	0.31 ± 0.01	91.8 ± 16.8	3.83 ± 0.36
50–100	19.4 ± 0.9	0.66 ± 0.03	0.31 ± 0.03	303.3 ± 77.6	9.69 ± 1.49
Total: 0-100				545.0 ± 113.4	20.73 ± 1.77
Total: 0-250				1309 ± 270	51.5 ± 5.52

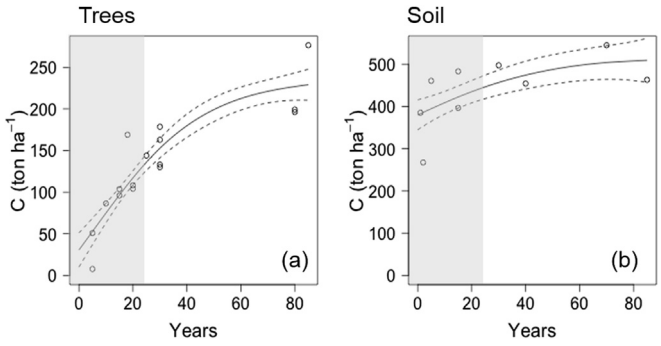

Fig. 3. Carbon (C) stocks (Mg ha^{-1}) after mangrove replantation for (a) trees and (b) soil in Matang Mangrove Forest Reserve. Tree data was estimated from published biomass values from Ong et al. (1984), Gong et al. (1984), Putz and Chan (1986), Alongi et al. (2004), Goessens et al. (2014), and Hazandy et al. (2014). Soil data is from this study and those estimated from C values in Alongi et al. (2004).

24.6 ± 1.8 Mg N ha^{-1} in the reference forest (Table 4). The clear-cut forest had 57% of the C and 37% of the N of the reference forest, suggesting that tree clear-cutting causes the loss of more than half of the total mangrove ecosystem C, and more than a third of the ecosystem N within a year. In the first 10 years, rates of C accumulation were 9.5 Mg C ha^{-1} yr^{-1}, after which rates decreased to 2.8 Mg C ha^{-1} yr^{-1}.

3.5. Pathways of C accumulation and loss

The mangrove soil had a mean $\delta^{13}C$ value of −28.6 ± 0.04‰ (range = −27.6 to −29.9‰) and $\delta^{15}N$ value of 3.1 ± 0.1‰ (0.9–8.8‰). The $\delta^{13}C$ values in the soil were close to those of mangrove litter, which were −29.4 ± 0.1‰, consistent with a mangrove origin for the soil OC (Fig. 4). For $\delta^{15}N$, relatively large differences between sites were evident for soils (1.3–6.2‰), but they were all well within the values of mangrove litter. Isotope values from phytoplankton were variable, but in general higher in $\delta^{13}C$ compared to the mangrove soil. Phytoplankton $\delta^{15}N$ (mean = −25.5 ± 0.8‰, 30.4 to −21.1) were similar to those of mangrove litter (mean = 6.1 ± 0.7‰; 1.1–9.2‰).

Comparing soils averaged across 0–100 cm depths, the clear-cut forest soils had a significantly higher mean $\delta^{13}C$ value (−28.09 ± 0.02‰) than the rest of the sites ($F_{5,\ 8.9} = 20.48$, $p < 0.001$; Fig. 4a). For $\delta^{15}N$, the clear-cut mangrove soil, and those of the 5-year old and 40-year old forests had significantly higher values (> 3‰) compared to soils of the 16-year forest, 30-year forest and the reference forest ($F_{8,\ 9.5} = 6.36$, $p = 0.007$; Fig. 4). The N:C values were not significantly different among sites ($p = 0.065$) or depths ($p = 0.093$), although the clear-cut site and the 40-year old site had notably higher N:C in the first 50 cm of sediment of soil compared to the

Table 4
Ecosystem carbon and nitrogen stocks (soil up to 1 m in depth; MgC ha^{-1}) of mangrove forests of different ages in Matang Mangrove Forest Reserve, Peninsular Malaysia. Tree C stocks were obtained from Alongi et al. (2004), Goessens et al. (2014), and Hamid et al. (2015).

	Clear-cut	5 yrs.	15 yrs[a]	30 yrs.[b]	40 yrs.	70 yrs.
C stock	385.2 ± 72.6	472.0 ± 15.0	679.5 ± 22.2	703.0 ± 22.3	630.3 ± 24.5	895.8 ± 113.9
N stock	15.7 ± 1.8	17.6 ± 1.1	19.6 ± 0.6	20.6 ± 0.8	21.2 ± 0.8	24.6 ± 1.8

[a] After one round of thinning.
[b] After two rounds of thinning.

rest of the sites (Fig. 4c). Among soil depths, $\delta^{13}C$ was about 0.6‰ enriched in the deep sediment compared to the surface ($F_{8,\ 40.3} = 3.51$, $p = 0.005$). Finally, $\delta^{15}N$ values were not significantly different within depths ($F_{8,\ 24.6} = 1.91$, $p = 0.104$; Fig. 4b). The clear-cut site was notably different from the rest of the sites, with higher $\delta^{13}C$, $\delta^{15}N$ and N:C values. In general, mangrove soils were depleted in $\delta^{13}C$, $\delta^{15}N$ and decreased in N:C with age, consistent with decreased decomposition (Table 2S).

4. Discussion

One year after tree harvest, mangrove ecosystem C and N stocks were halved. In the first ten years, the forest recovered quickly with rates of C accumulation of 9.5 Mg C ha^{-1} yr^{-1}, primarily as a result of rapid tree and root growth in this humid-warm and nutrient-rich environment. After ten years, the rate of accumulation decreased to 2.8 Mg C ha^{-1} yr^{-1}. Forty years after replanting, mangroves were still a 26% lower in C and 15% lower in N compared to the reference forest.

After tree harvest, soil $\delta^{13}C$ values significantly increased throughout the sediment column, an effect likely due to decomposition (Nadelhoffer and Fry, 1988; Adame and Fry, 2016). In the surface, increased $\delta^{13}C$ values could also partly reflect increased benthic microalgal photosynthesis in the newly open forests (Lovelock, 2008). Mangroves in MMFR have respiration rates of 0.5–1.8 Mg C ha^{-1} yr^{-1}, and oxidation rates of 3.4–5.2 Mg C ha^{-1} yr^{-1} (Alongi et al., 2004). Our measured rate of loss of soil C after perturbation of 3.1 Mg C ha^{-1} yr^{-1} is well within these expected ranges.

Nitrogen dynamics followed a similar pattern to C variations. The N budget in mangrove forests is primarily the sum of outputs (denitrification-nitrification, plant uptake) and inputs (N fixation and sediment burial). MMFR has denitrification rates of 0.04–1.1 Mg N ha^{-1} yr^{-1}, plant uptake of 0.8–2.3 Mg N ha^{-1} yr^{-1}, sediment burial of 0.3–0.4 Mg N ha^{-1} yr^{-1} and low N fixation rates, which ranged from undetectable to 0.3 Mg N ha^{-1} yr^{-1}, (Alongi et al., 2004). In general, mangrove forests of MMFR are considered sinks of 0.8–3.5 Mg N ha^{-1} yr^{-1} (Alongi et al., 2004). Our estimated net ecosystem N uptake rate after restoration is between 0.1 and 0.6 Mg N ha^{-1} yr^{-1}, values within the lower end of measurements by Alongi et al. (2004).

The years between tree harvest and replantation are critical for N and C losses. In cleared mangroves, the sediment becomes oxygenated, which causes the rapid decomposition of organic matter, increased respiration, decreased denitrification, and decreased sediment burial, all of which results in C and N loss (Rivera-Monroy and Twilley, 1996; Alongi et al., 1998; Sidik and Lovelock, 2013). After replantation, soil $\delta^{13}C$ values stabilized around −29‰, a value similar to mangrove litter. It is likely that at after replantation, a gradual shift from aerobic to anaerobic soil conditions occurs, with anaerobic reactions such as sulphate reduction dominating (Alongi et al., 1998) and limiting C loss. Regrowth of roots following tree replantation may account for most of the early (< 5 years) recovery of soil C stocks (Adame and Fry, 2016; Adame et al., 2017).

In the first five years, soil C accumulation rates were between 2.9 and 6.1 Mg C ha^{-1} yr^{-1}, which were twice as large as those in mature forests (> 50 years) that were ≤1.2 Mg C ha^{-1} yr^{-1}. Our estimates of C accumulation in mature forests were similar to previous assessments of soil OC accumulation of 2–2.5 Mg C ha^{-1} yr^{-1} in planted forests in MMFR estimated with ^{210}Pb (Alongi et al., 2004), 0.7–4.9 MgC ha^{-1} yr^{-1} in mangrove forests in French Guiana (Marchand, 2017) and 0.4–1.8 MgC ha^{-1} yr^{-1} in mangroves in Mexico (Adame et al., 2015a). Mangrove OC and N accumulation followed a logarithmic trajectory for soil, trees and litter, with highest sequestration rates in the early years. Similarly, the increase in the soil layer resulting from mangrove progression followed a logarithmic trajectory in French Guiana for mangroves from 3 to 48 years old (Marchand, 2017). This result highlights that restoration projects should be valued considering different C uptakes between young and mature forests (Alongi, 2011).

Despite our described progression of C and N accumulation with time, natural factors are likely to contribute to spatial and temporal variations. Mangroves are constantly perturbed by natural factors, such as tropical storms which can cause extensive damage to trees (Sherman

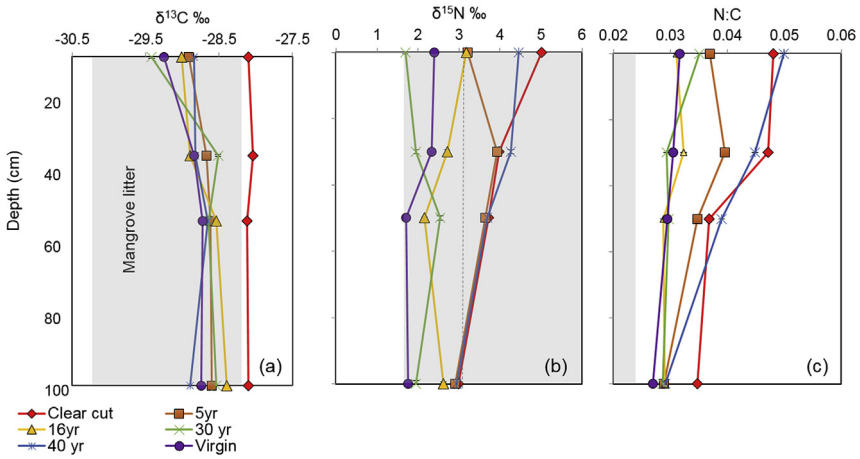

Fig. 4. (a,b) Isotope values ($\delta^{13}C$ and $\delta^{15}N$; ‰) and (c) N:C values of soils in mangrove stands of different ages and depths in Matang Mangrove Forest Reserve, Malaysia. Each value represents the mean ± standard error of 3–5 plots. The shaded area indicates values of mangrove litter (range).

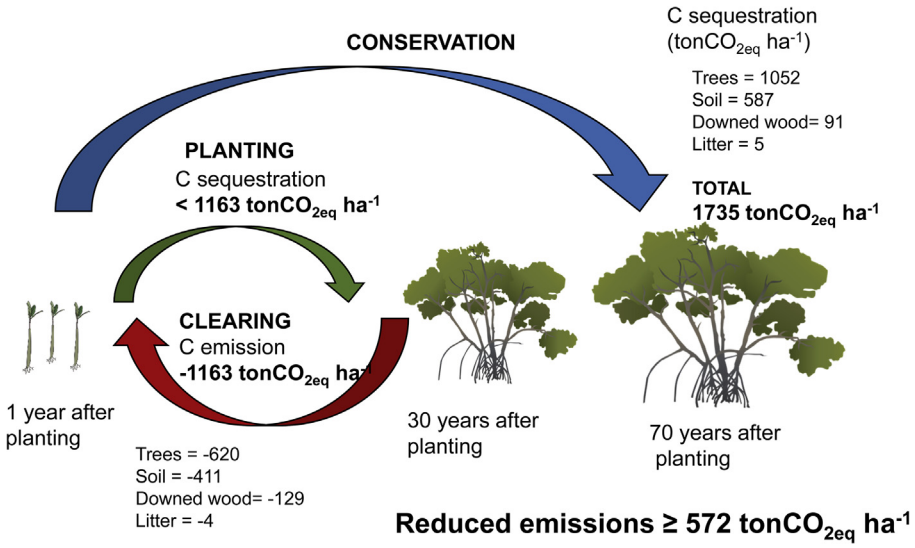

Fig. 5. Conceptual diagram of avoided emissions resulting from changes in land use practices from clear cutting-planting mangroves to conservation in Matang Mangrove Forest Reserve, Peninsular Malaysia.

et al., 2001; Kauffman and Cole, 2010) and peat collapse (Cahoon et al., 2003). Many mangroves can naturally recover after such perturbations if the conditions are adequate, but some stands may never return to their original condition (Sherman et al., 2000; Baldwin et al., 2001). Additionally, mangrove C accumulation is closely related to sea level (Krauss et al., 2013; Lee et al., 2014), which will increase in the coming decades. Thus, the establishment of mangrove forests and their rapid rates of C and N sequestration do not guarantee continual delivery of this ecosystem service. Based on our results, planted mangroves can recover relatively quickly, but only if the conditions are adequate.

Carbon and N stocks typically follow a progression with age. However, we found variability within a few sites. The 40-year old forest supports mixed *Rhizophora* and *Brugueira* species, and has been conserved for educational purposes and is close to the town of Sepatang. This forest at 40 years had lower C stocks than the managed forests at 30 years. Thus, despite differences in age, the spatial variability within sites, such as nutrient inputs, management, and climate will affect C and N sequestration potential for different mangrove forests.

The differences among sites with age in C and N content can be translated into delivery of ecosystem services. For example, our reference had twice as much downed wood as the rest of the forests. Downed wood could be an important habitat for fauna in mangrove forests (Allen et al., 2000; Feller and Chamberlain, 2007). Thus, restoration of mangroves, as with any other ecosystem, might have resulted in a novel type of forest (Hobbs et al., 2009) with lower habitat diversity.

Our results provide valuable information on the rates of loss and recovery of C and N after mangrove clearing and replantation in Malaysia. However, the comparison with other mangrove forests needs to be made with caution, because variability within environmental factors and management practices will strongly affect C and N sequestration rates. Mangroves in Asia Pacific are very productive and have the highest soil C stocks on Earth (Atwood et al., 2017). In MMFR conditions for mangroves are ideal, with warm temperatures, high rainfall and high nutrients; factors contributing to high forest productivity (Reef et al., 2010). Additionally, replantation of the mangroves in the MMFR occurs in soil with conditions highly suitable for plant growth. Rates for C and N gains are likely to be lower for other mangrove forests in less productive locations. In some cases, C and N gains could be close to zero if the soil has been strongly perturbed and the conditions for plant growth are inadequate (Kodikara et al., 2017). Nevertheless, in this study, we describe the best account to date for long-term C and N loss and sequestration rates in mangrove forests.

4.1. Implications for the Matang Mangrove Forest Reserve

The MMFR has been successfully managed for forestry for over a century. At the moment, there are plans for reducing the harvesting cycle from 30 to 20 years to increase charcoal wood supply. However, with concerns of decreased tree productivity and the decline on the price of charcoal, C markets could be an attractive option (Ullman et al., 2013; Ammar et al., 2014).

The current management program releases 1163 $MgCO_{2eq}$ ha^{-1} after mangrove clearing. After replanting, the forest recovers relatively quickly in the first ten years, although there is likely to be a small loss of carbon every clearing-planting cycle which results in lower C stocks in the managed versus the reference forest (Fig. 5). If instead of clearing and planting, the forest is protected and left to recover for 70 years, it will sequester 1735 $MgCO_{2eq}$ ha^{-1}. The protection of the mangroves compared to the business-as-usual scenario in which the forest is continuously clear-cut and planted, will provide reduced carbon emissions of 572 $MgCO_{2eq}$ ha^{-1} (Fig. 5). The reduced carbon emissions could be worth $USD 4574 based on a C price of $USD 18 per Mg. If 1000 ha of mangroves were protected, the revenue is $USD 4.6 million in 40 years, or $USD 114,348 per year. In addition to the avoided emissions, the conservation of mangrove forests will provide habitat for birds, improved fisheries, and coastal protection, which could also be considered in the future for payments for ecosystem services (PES, Locatelli et al., 2014).

The sustainable management of the MMFR has allowed for productive mangroves to be maintained in this region for over a century. The rates of loss and gain of C and N estimated in this study could facilitate the inclusion of mangroves in emerging C and N markets. These results could also provide an incentive for the protection, restoration, and sustainable management of mangrove forests in the Indo-Pacific region and in similar mangrove forests throughout the world.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2018.04.019.

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